Habitat use and population dynamics of brown bears (Ursus arctos) in Scandinavia

JONNA KATAJISTO

Helsinki 2006

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Academic dissertation

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The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I Katajisto, J., Moilanen, A. and Swenson, J. E. 2006. Landscape-level habitat use by brown bears (*Ursus arctos*) in relation to human distribution in Scandinavia. - *Submitted*.

II Katajisto, J. and Moilanen, A. 2006. Kernel-based home range method for data with irregular sampling intervals. - Ecological Modelling 194: 405-413.

III Katajisto, J. and Moilanen, A. 2006. Bayesian estimation of habitat weighted kernel home ranges. - *Submitted*.

IV Katajisto, J., Ovaskainen, O. and Swenson, J. E. 2006. The role of sexually selected infanticide in the reproductive biology of the brown bear (*Ursus arctos*). - *Submitted*.

V Katajisto, J., Moilanen, A., Wiegand, T. and Swenson, J. E. 2006. Effects of targeted harvesting on Scandinavian brown bears. - *Manuscript*.

The following table shows the major contributions of authors to the original articles

	I	II	III	IV	V
Concept	JK, JS	JK, AM	AM, JK	JK, JS	JK, JS
Methods and implementation	JK, AM	AM, JK	JK, AM	OO, JK	JK, AM, TW
Data	SBBRP	SBBRP	SBBRP	SBBRP	SBBRP
Analyses	JK	JK, AM	JK	JK	JK
Manuscript preparation	JK, JS	JK, AM	JK, AM	JK, OO, JS	JK, AM, JS

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Contents

Aristotle said 'For the things we have to learn before we can do them, we learn by doing them'

Summary

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"Arguably, no group of organisms offers more challenges to conservation biology and conservation politics than large carnivores. These animals, in accord with how they make their living, are big and fierce."

(Noss et al. 1996)

1. Introduction

1.1. Conservation and management of large carnivores

Humans are increasingly entering carnivore habitats and at the same time populations of large carnivores recovering from past extirpation efforts are becoming involved in mutually threatening interactions with humans. Many populations of large carnivores escaped extinction during the twentieth century owning to legal protection, habitat restoration and changes in public attitudes (Breitenmoser 1998, Treves et al. 2004). Successful management has resulted in gradual recovery and return of carnivores to their original habitats, which has lead to carnivore-human conflicts and damages to livestock in many areas worldwide (Mech 1995, Mattson et al. 1996, Breitenmoser 1998, Servheen et al. 1999, Kojola & Kuittinen 2002, Garshelis & Hristienko 2006). For large carnivores to have a long term future we have to allow them to reoccupy some of their former habitats, which means integrating them into the landscapes where humans live. This makes the conservation of large carnivores particularly challenging.

Major threats or obstacles for bears and large carnivores in general are negative attitudes, human-caused mortality and deterioration of habitats (Swenson et al. 2000). Together with legal harvest and poaching vehicle collisions are a significant source of human-caused mortality (Revilla et al. 2001, Hebblewhite et al. 2003). Roads also hamper animal movements, decrease the habitat quality and increase the accessibility of poachers to wild animals (Mace et al. 1996, Noss et al. 1996, Merrill et al. 1999, Cramer & Portier 2001, Revilla et al. 2001, Kerley et al. 2002, Kramer-Schadt et al. 2004). Negative attitudes towards predators originate mainly from conflicts with domestic animals, mostly sheep and semi-domestic reindeer as well as hunting dogs (Sagør et al. 1997, Breitenmoser 1998, Naughton-Treves et al. 2003, Ogada et al. 2003). Additionally, poaching is primarily motivated by damage to domestic animals together with perceiving carnivores as competitors for ungulate game (Andren et al. 2006). Large carnivores are also often perceived as a threat for human safety. A key for conservation of large carnivores seems to be reduction in damages to livestock as well as better understanding of the values, beliefs, and demands of those who are involved or affected (Breitenmoser 1998, Woodroffe 2000, Bowman et al. 2004, Mattson et al. 2006).

Various methods for human coexistence with large carnivores have been suggested, ranging from barriers and repellents based on unpleasant olfactory or visual stimuli to translocation of carnivores (Linnell et al. 1997, 1999, Musiani et al. 2003, Treves & Karanth 2003). Wildlife management is often viewed as a discipline oriented towards seeking sustainable strategies of wildlife exploitation, whereas conservation is more concerned with the long-term preservation of species and their habitats (Festa-Bianchet & Apollonio 2003). Although these objectives may appear contradictory, in case of large carnivores the management is an important component of conservation. Removal of problematic individuals and harvest belong to the toolbox of carnivore control. However, recreational harvest or targeted killing of some individuals has often failed to remove the problem (Sagør et al. 1997, Herfindal et al. 2005, Berger 2006). Reduction of population size with regulated harvest can reduce confrontations with humans and livestock, but this is problematic in case of already small populations. Although lethal control remains an essential tool in carnivore management, it can not be the final solution for coexistence with large carnivores.

Large carnivores tend to occupy large home ranges and thus require large areas. In Europe there are few, if any, wilderness areas with suitable habitat and size large enough to maintain populations of large carnivores without human contact (Linnell et al. 2000). Therefore the conservation and management of carnivores is based on their integration into human-dominated multi-use landscapes and the long-term survival of carnivores is dependent on areas outside protected reserves (Linnell et al. 2000, Schadt et al. 2002). Consequently, better land-use planning and novel approaches such as development of structures for highway crossing may turn out essential in carnivore conservation (Noss et al. 2002, Carroll et al. 2003, Clevenger & Waltho 2005). Of utmost importance in development of such non-lethal management strategies for large, wide-ranging carnivores is the understanding of species-specific behaviour and interactions with surrounding habitats.

1.2. Brown bears

The brown bear (*Ursus arctos*), the most widespread bear in the world, is found across Europe, Asia and North America in habitats ranging from forests to dry deserts and tundra (Servheen et al. 1999, Swenson et al. 2000, Schwartz et al. 2003). Despite such adaptability, large populations in Europe are nowadays only found in the eastern and northern parts of Europe. Elsewhere in Europe human activities have resulted in small and isolated populations (Swenson et al. 2000, Zedrosser et al. 2001).

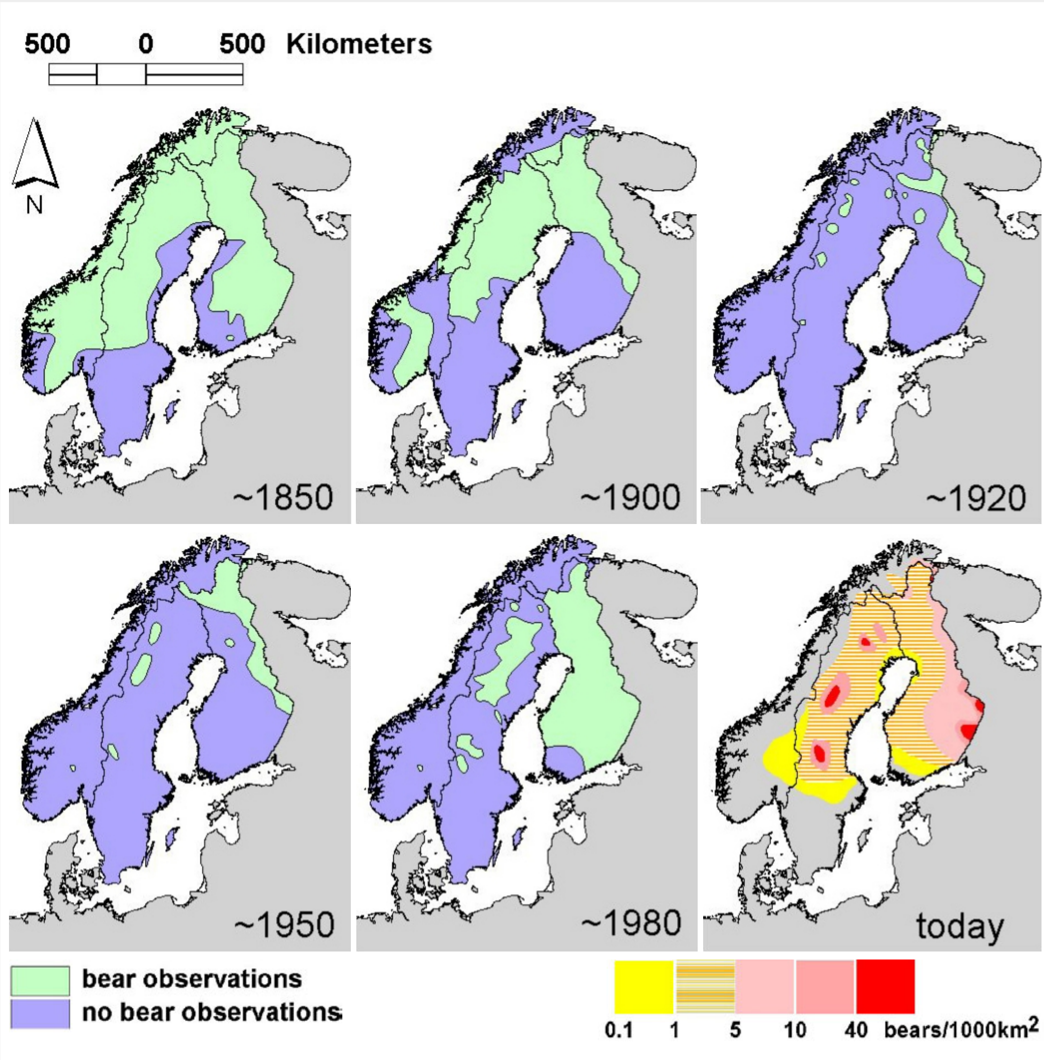
Brown bears are solitary carnivores that use large areas during their lifetime. Adult bears establish lifetime home ranges that may overlap to varying degree depending on the sex and relatedness of the individuals, and home ranges of males are larger than those of females (McLoughlin et al. 1999, Dahle & Swenson 2003a, b, Støen et al. 2005b). The size of a bear's annual home range in Scandinavia varies from 200 km^2 for adult females to over 1000 km^2 for adult males (Dahle & Swenson 2003a, 2003b). A majority of the males disperse from their natal areas, whereas females are more philopatric and often establish home ranges that overlap or are adjacent to their natal areas (Blanchard & Knight 1991, McLellan & Hovey 2001, Kojola et al. 2003, Støen et al. 2005a). However, in an expanding population also females have been shown to disperse, although not as far as males (Swenson et al. 1998b, Kojola & Laitala 2000). In Scandinavia, males generally disperse at the age of two years, whereas females tend to leave at the age of three years (Støen et al. 2005a).

The age of sexual maturity for both sexes varies between 4 – 6 years (McLellan 1994, Zedrosser et al. 2004). The earliest recorded age at first reproduction is 3 years (Zedrosser et al. 2004). During the mating season in mid-May to early July bears increase their range size and females may mate with several males as well as males with several females (Craighead et al. 1995, Dahle & Swenson 2003b, Schwartz et al. 2003). The ovulation of female bears is induced by behavioural, hormonal or physical stimulus (Boone et al. 1995, Craighead et al. 1995). The litter consisting of 1-3 and occasionally 4 cubs is born in the winter den in January to March. Cubs typically follow their mother over the next wintering period and separate from the mother during the following spring, sometimes rarely females keep their litter even as long as 3.5 years, although in Scandinavia only maximally for 2.5 years (McLellan 1994, Swenson et al. 2001, Schwartz et al. 2003). Bears may live older than 30 years, but reproductive senescence occurs in females at an age of around 27 years (Schwartz et al. 2004).

Only females take care of the offspring and when accompanied by a litter they are not receptive to males, which leads to a minimum interval of two years between successful litters. Consequently, male bears may benefit from the killing of the young by gaining a mating opportunity with the mother, thereby exhibiting sexually selected infanticide (SSI)

Box 1. Return of the bear

The recent history of the Scandinavian brown bear goes from near extinction to population recovery and expansion through successful management (Swenson et al. 1994, 1995, 1998a). The current population size estimate in Sweden is 2350 - 2900 individuals (Kindberg & Swenson 2006). The development of the nearby Finnish population follows about the same pattern (Nyholm & Nyholm 1999, Kojola & Laitala 2000). Based on bounty data there were 4000 – 5000 bears on the Scandinavian Peninsula around 1850, and over 1000 bears in Finland. As the policy at that time was to exterminate bears, by 1930 bears were virtually extinct from Norway and only 130 individuals had survived the overexploitation in four small remnant areas in Sweden (Swenson et al. 1995, 1998a). As the turn of the century, national parks were established and killed bears became Crown property in Sweden, which removed the economic incentive to kill them. As a response to reduced mortality, the population grew quickly and expanded in spite of continuing habitat change due to intensive forestry (Swenson et al. 1998a).



(Hrdy 1979, Hrdy & Hausfater 1984, Packer & Pusey 1984). Infanticide is classified as SSI if the perpetrator is not the father of the young it kills, if killing of the young shortens the time to the female's next oestrus, and if the perpetrator has a high probability of siring the female's next litter (Hrdy & Hausfater 1984). These three requirements have been documented in brown bears in Scandinavia (Bellemain et al. 2006), and the occurrence of SSI or counter-strategies related to it have been documented in various brown bear populations (Wielgus & Bunnell 1995, Swenson et al. 1997, 2000, 2001). Female brown bears have counter-strategies to avoid SSI, such as multi-male mating and use of suboptimal habitats, together with movement and activity patters that differ from those of males (Wielgus & Bunnell 1994, 1995, 2000, Swenson 2003, Ben-David et al. 2004, Bellemain et al. 2006).

Feeding habits of bears vary between seasons. Although during spring bears are significant predators of ungulates in some areas, the main source of yearly energy consumption are berries which constitute most of their diet in the autumn before hibernation (Dahle et al. 1998, Persson et al. 2001). Also ants form a significant portion of bears food in boreal forests (Swenson et al. 1999).

1.3. Scandinavian Brown Bear Research Project

The Scandinavian Brown Bear Research Project (SBBRP) collared its first bear in 1984 with an objective to study the basic ecology of brown bears. To date the project has followed more than 400 bear individuals, many from birth to death. This material

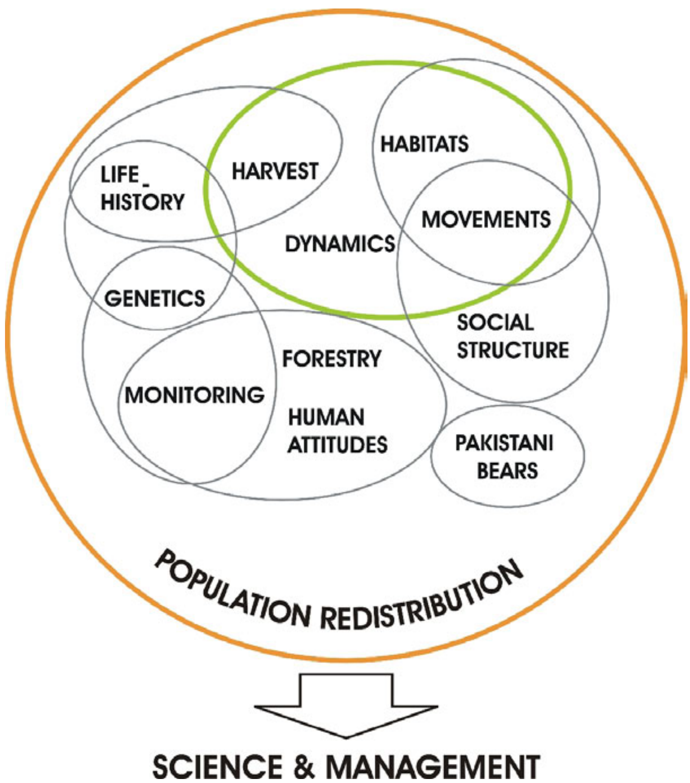


Figure 1.

How some of the central topics studied within Scandinavian Brown Bear Research Project are shared between students (ellipses). Common for all the topics is that they all aim to better understand the factors determining the distribution of bear populations that is essential for sound scientifically based management of bears. The green ellipse points up themes that have motivated this thesis (see 1.5.).

has been utilized in investigations regarding many aspects of the life-history, behaviour, genetics and population biology of bears as a model for large carnivores. The SBBRP has contributed significantly to the conservation and management of brown bears at the European level, and has also collaboration with North American research projects. Most of the knowledge about bears presented above is due to the SSBRP. Several PhD and MSc projects form the backbone of the research currently done in the project. Although these projects also have their own objectives, they aim to build on the previous research in the project, so that each student with a different background adds to the knowledge of bear biology and to the understanding of population ecology and management of large carnivores in general (Fig. 1). The main areas of focus in the SBBRP currently are: (i) the consequences of harvesting on population dynamics, and (ii) its role as a selective pressure in bear life history, (iii) habitat selection and the effects of forestry, (iv) density-dependent population regulation, (v) genetic components of fitness, and (vi) development of population monitoring techniques. The common goal is to understand factors affecting population distribution, which is essential for the successful management of bear populations and avoidance of conflicts with humans, also outside Scandinavia.

1.4. Study areas and data collection

The Scandinavian Brown Bear Research Project has conducted intensive radio tracking in two study areas, one located in northern Sweden (67°N, 18°E, 8000 km^2) and the other in central Sweden and south-eastern Norway (61°N, 18°E, 13000 km^2) (Swenson et al. 1998b, Dahle & Swenson 2003a, b). Boreal coniferous forests with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) dominate both study areas, although lakes and bogs cover large areas especially in the south. Mountains with sub-alpine habitats with birch (*Betula pubescens*) cover parts of the northern area. Elevations range from 200 m in the south to above 2000 m in north. Both study areas are sparsely populated by humans. For a detailed description of the study areas see (Zedrosser et al. 2006). Legal harvest has been allowed within both study areas throughout the study period, but the northern area includes three national parks, in which hunting is prohibited. Harvest season is in the autumn from 21 of August until 15 October (or 15 September in the north). The total harvest is limited by a quota set by the authorities for each of the ten counties where hunting is allowed. All hunters must report bears that are killed or wounded within 24 hours. When the quota is met, the season is closed with a 24-hour notice. Females that are accompanied by a litter are protected from the harvest. Hunters report the location, sex and weight of the killed bear. Hair samples and a premolar tooth from all hunter-killed bears are sent for further DNA analysis and age determination (Matson et al. 1993).

Bears were captured in the spring shortly after den emergence by immobilizing them from a helicopter using a remote drug delivery system (Dan-Inject®). The drugs and protocol used in immobilization are described in Arnemo (2005) and Arnemo et al. (2006). Adult individuals were equipped with neck-mounted VHF radio transmitters (Telonics®). A sterile radio transmitter was implanted in the peritoneal cavity of yearling females following a well established biomedical protocol (Arnemo 2005). Thus the female young of marked mothers were followed from the birth. All captured bears were weighted and measured, and blood, hair and tissue samples were taken for the later analysis. For animals that had not been followed from birth, a premolar tooth was removed for age determination (Matson et al. 1993). Radio-marked bears were located on average once a week from an aircraft or from the ground using receivers and handheld or aircraft-mounted antennas during their entire active period from April to October (Dahle & Swenson 2003a, 2003b). The reproductive state of radio-tracked females, i.e. the number and age of cubs following the female, was systematically monitored from an aircraft or the ground after females emerged from their winter dens, after the end of the breeding season (early July) and before entering the den. Bears were normally monitored until death or transmitter failure. All capture and handling conformed to the current laws regulating the treatment of animals in Sweden and were approved by the appropriate Swedish ethical committee (Djuretiska nämden i Uppsala).

1.5. Questions that have motivated this thesis

The conclusions of previous studies from the SBBRP describing the pattern of population expansion discovered the need to investigate the role of space-use and population dynamics in the ecology of Scandinavian bears. Coming from a department with a strong background in spatial ecology and population modelling, the obvious choice for my

PhD project was to address large-scale spatial aspects and to use modelling as a tool for answering some of the hottest bear management issues in Scandinavia today. These include questions such as what is a suitable habitat for a bear? How are these habitats distributed and are there still suitable unoccupied areas for bears? Is the bear population more vulnerable to increased harvest of some particular kinds of individuals? In order to assess these issues I aimed at developing and parameterising an individual-based model for simulating bear population dynamics, which could later be expanded to a spatially realistic predictive model.

2. Main results and discussion

2.1. Habitat use

Use of models to understand and predict the distribution of a species is an important step in planning the conservation and management of wildlife (Pearson et al. 1999). Habitat models and resource-selection functions are useful methods for analysing habitat relationships (Boyce & McDonald 1999, Schadt et al. 2002, Larson et al. 2003, 2004, Guisan & Thuiller 2005). Large carnivores typically require large areas for their home ranges, which often results in conflicts with humans competing for the same space (Noss et al. 1996, Breitenmoser 1998, Woodroffe & Ginsberg 1998, Revilla et al. 2001). Consequently, their conservation requires landscape-level management of often multi-use habitats (Merrill et al. 1999, Linnell et al. 2001, Preatoni et al. 2005).

Space use by an animal is described by its home range or utilisation density distribution (UD); an area with a spatially defined probability of occurrence of the animal during a specific time period (Powell 2000, Kernohan et al. 2001). Home ranges estimated from radio location (or GPS) data often form a framework for analysis of animal movements and habitat selection, and good estimates of home ranges can thus provide interesting insight into many basic topics in animal ecology. Chapters **I**, **II** and **III** in my thesis deal with landscape-level habitat assessment for bears and the development of improved kernel methods for estimating home ranges.

The brown bear population in Scandinavia has been increasing and expanding its range during the last decades (Swenson et al. 1994, Swenson et al. 1995). Consequently, it is important to evaluate the distribution of areas suitable for bears, occupied and yet unoccupied by the population. Brown bear home ranges are not randomly distributed over the landscape, but occur mainly in forested areas with a low level of human influence, as defined by the human influence index we developed for Scandinavia (**I**). Avoidance of humans is apparent both in the northern and southern study areas in Scandinavia, even though the general level of human influence is much lower in the north (**I**). This suggests, that instead of having a strict threshold, bears avoid humans relative to the level of surrounding human influence, at least in the case of an expanding bear population and Scandinavian levels of human influence. The best 50% of the habitats based on the quantitative habitat model for bears (**I**) cover approximately 115 000 km^2 of the Scandinavian peninsula (Fig. 2). Based on bear observations and our habitat model, bears apparently already occupy most of the areas with good habitat in Sweden, except an isolated area in southern Sweden that is separated from the occupied area by a dispersal barrier formed by large lakes and high human influence (Fig. 2). There are large areas of suitable unoccupied habitats in south-eastern Norway.

Radio-telemetry data obtained by traditional triangulation methods (Box 2) often contain periods of frequent observations within a time series of temporally more isolated and independent observations. The utilisation density distribution (UD) is an estimate of the proportion of time spent at any location inside an animal's home range. Consequently, using such partially temporally aggregated data overemphasises areas of frequent sampling in the UD estimate. On the other hand, loss of data results if data is standardized into regular temporal intervals by resampling only locations that have at least a given time interval between them (**II**)(Rooney et al. 1998). Instead, data can be weighted so that if an independent observation temporally distant from other observations is given a relative weight of one, then observations in a temporally aggregated cluster are given weights less than one. However, the total weight of such a cluster exceeds one, as it contains more information than just an individual observation would (**II**, **III**) (Fig. 3). Simulation experiment with known UDs shows that such a weighted kernel estimate performs better than an estimate that uses resampled data (**II**).

In addition to having problems with temporally autocorrelated data, kernel estimates are sensitive to the degree of smoothing that has been chosen (Silverman 1986, Worton 1989, Seaman & Powell 1996). A too wide kernel width spreads the estimate and conceals details of the internal structure of the home range, whereas narrow smoothing results in unrealistic peaks and leads to a discontinuous estimate. Furthermore, kernel estimators have been criticised for ignoring sharp edges and spreading the home range unrealistically to unused habitats, and thus, overestimating the size of the home range (Seaman et al. 1999). The latter problem can be overcome by modifying the kernel with a preference multiplier for each habitat type (**III**). Using a novel likelihood-based Bayesian approach in estimating these habitat multipliers simultaneously with the kernel width from the location data provides a way of incorporating effects of habitat quality and parametric uncertainty into home range estimates (**III**). Habitat multipliers reflect the animal's habitat preference accounting for habitat availability. Additionally, a Bayesian estimate of the home range structure is obtained. When applied to brown bears, our approach results in smaller estimated effective home range sizes and apparently more realistic home range layouts (**III**, Fig. 3). This is because the UD does not spread into presumably poor habitats adjacent to animal observations, such as agricultural land and barren terrain bordering forest. Instead, the estimated UD concentrates more into preferred habitats, such as forest. An

Box 2. Traditional triangulation

Most of the location data were obtained using standard triangulation (White & Garrott 1990, Rodgers 2001), i.e. the location of the bear with the transmitter was estimated by taking at least three directional bearings from known locations (normally from roads) and the animal was assumed to be located at the intersection of the bearings (or within the middle of the formed triangle) (see the figure below). The error in the localisation depends on the habitat (topography etc.), distance from the transmitter, and the movements of the individual between the measurements. The mean error in the positions obtained with triangulation in this study was 452 m ± 349 m (SD), when the bearings were taken from 400 – 2200 m distance from the transmitter (B. Dahle unpublished data).

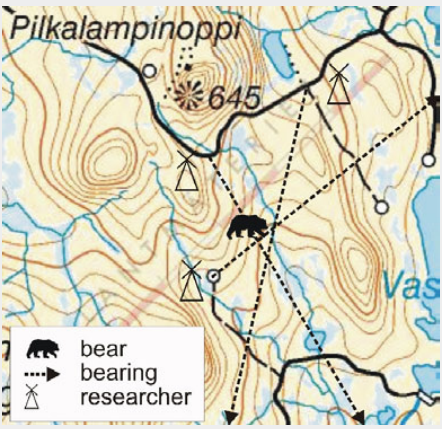


Figure B1.

An example of how the bearings are taken to locate the radio-marked bear.

The main limitation of the triangulation technique is the signal range of the transmitter, which varies from a couple of kilometres to about 20 km depending on the landscape. Because bears move over large areas, locating bears by triangulation is limited by searching time and access to remote areas. Consequently, it is virtually impossible to collect location data with regular time intervals or simultaneously for many bears, and obtain equal representation of all the individuals in the data. Also, costs increase with increased frequency of the localization. For some specific studies more frequent data was collected for fewer individuals. Conventional methods of analysis have been limited in overcoming the challenge posed by such diverse records following from inherent shortcomings in the tracking protocol.

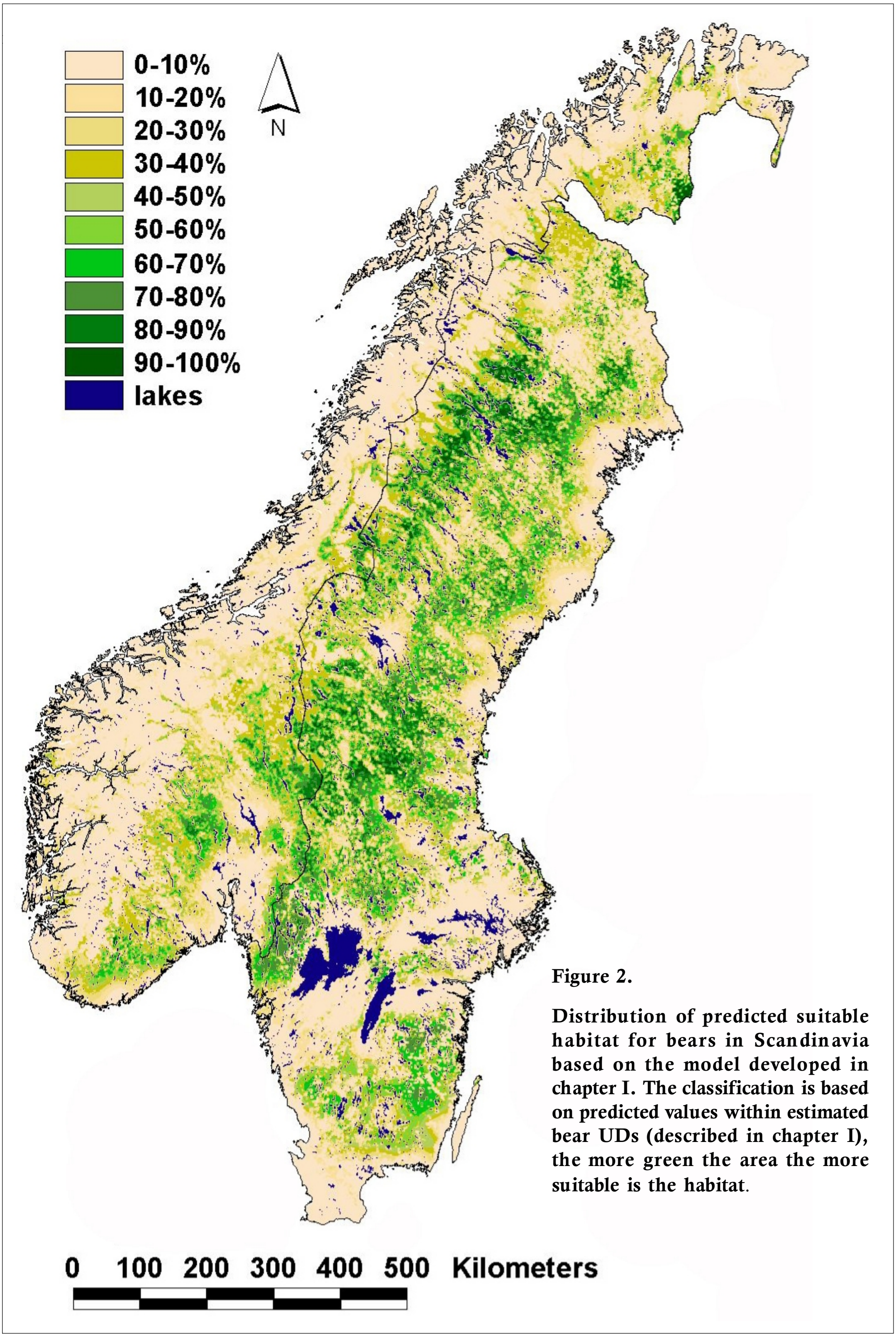


Figure 2.

Distribution of predicted suitable habitat for bears in Scandinavia based on the model developed in chapter I. The classification is based on predicted values within estimated bear UDs (described in chapter I), the more green the area the more suitable is the habitat.

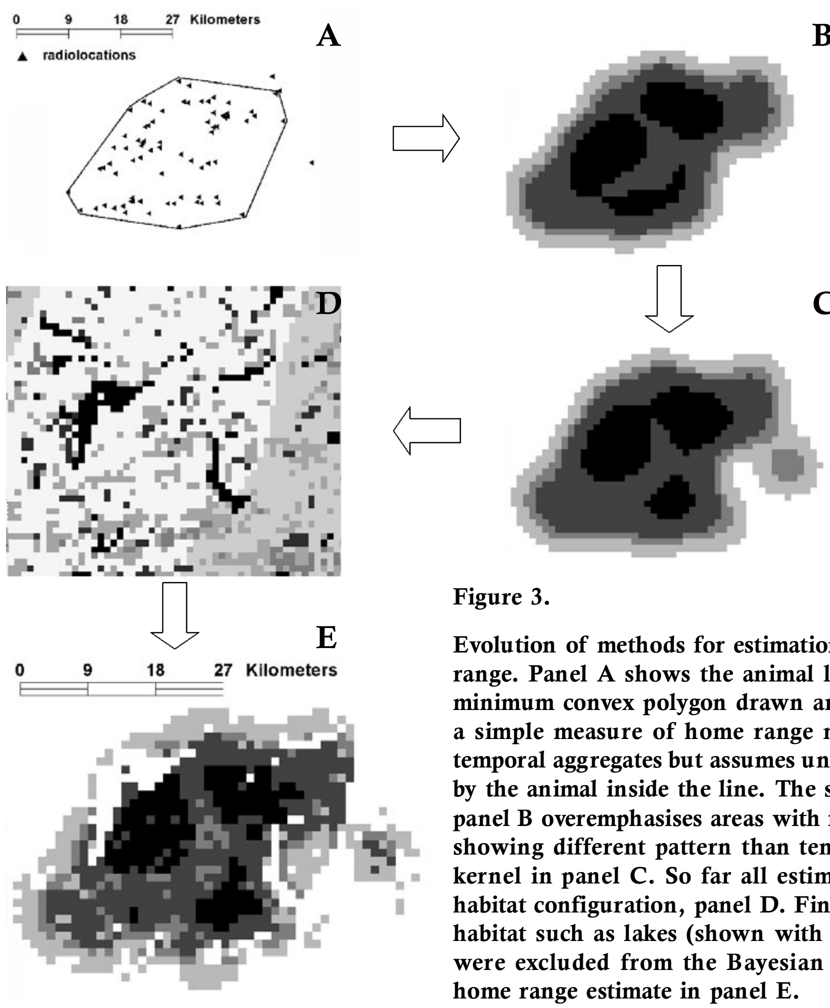


Figure 3.

Evolution of methods for estimation of animal home range. Panel A shows the animal locations and 95% minimum convex polygon drawn around them. Such a simple measure of home range may be robust for temporal aggregates but assumes uniform use of areas by the animal inside the line. The standard kernel in panel B overemphasises areas with frequent sampling showing different pattern than temporally weighted kernel in panel C. So far all estimates regarded the habitat configuration, panel D. Finally, unfavourable habitat such as lakes (shown with black in panel D) were excluded from the Bayesian habitat weighted home range estimate in panel E.

2.2. Population dynamics

The Brown bear population in Scandinavia has increased both in numbers and range after a population bottleneck in the early 1900s, even though conservative harvest has been allowed since 1943 (Swenson et al. 1994, 1995, 1998b). Sæther (1998) estimated an annual population growth rate of up to 16%. Concerns about the threats that an increasing bear population causes to humans and livestock have increased the pressure for controlling the population by raising the level of harvest.

The effects of harvest on population dynamics depend partly on the interaction between hunter selectivity and the mating system of the target species (Greene & Umbanhoward 1998). In polygynous species, such as bears, the strategy of selectively harvesting males has been considered to increase the sustainable yield (Swenson et al. 1997, Sæther et al. 2004). This is particularly widespread in the management of ungulates (McLoughlin et al. 2005). However, in some species, male-biased harvest may disturb the social structure of the population and induce sexually selected infanticide (SSI), reducing the survival of the offspring (Hrdy 1979, Whitman et al. 2004). Chapters **IV** and **V** cover quantification of the effect of SSI on litter survival and evaluation of different harvest schemes while accounting for SSI in Scandinavian brown bear population.

Large male bears are a popular trophy, which might skew hunting mortality in bears towards males

(Miller et al. 2003). The potential consequences of male-biased harvest in the social system of bears have been recognised only recently (Swenson et al. 1997). There are two opposing views of how male-biased harvest can affect the survival of cubs through SSI (McLellan 2005). First, it has been suggested that because males are prone to kill cubs, removing a large male from the population should generally increase the cub survival (Miller 1990, Miller et al. 2003). The opposing view is that removing a mature male increases the likelihood of a new male entering the area and killing the cubs that he has not sired (Swenson et al. 1997, 2001, Swenson 2003). Bayesian parameter estimation of a model of the reproductive cycle of females suggests that although removal of males by harvest increases cub mortality in Scandinavian bears, it does not have a major effect on the mortality of entire litters, possibly because females manage to protect part of their litter (**IV**). The ability of the female to avoid SSI increases with the female's experience (**IV**). As a consequence to population dynamics, cub mortality due to harvesting adult males does not necessarily shorten the time to the female's next oestrus and thus the extra cub mortality is not compensated by a shorter litter interval (**IV**).

When properly planned, hunting can be an important tool for bear management (Boyce et al. 2001). In addition to hunter selectivity, the behaviour of individuals may influence their susceptibility to being killed, and thus the response of the population to different types of harvest. In reality, selective harvest scenarios can be based on the size of the individual or on protecting females accompanied by a litter. We investigated the effects of increased hunting to the population growth and structure of bears in Scandinavia. We used three differently targeted harvest scenarios including random, male-biased and juvenile-biased hunting. Also the influence of allowing the hunting of females with cubs was evaluated. The analysis accounted for SSI and high demographic variance among individuals (**V**). Male-biased harvest has a positive influence on the population growth rate, whereas allowing the harvest of females with litter slightly decreases the population growth (**V**). Increasing the harvest from present 5% to 10% is unlikely to endanger the population (**V**). Some effects of changing the hunting policy will appear only after a time delay, which indicates that a gradual increase in hunting combined with monitoring of population growth would be a conservative and safe strategy to increase bear harvest in Scandinavia (**V**).

3. Synthesis and perspectives

In this thesis I have assessed the distribution of suitable areas for bears at the scale of Scandinavia and investigated their population dynamics, in addition to developing improved methods for analysing space-use and home ranges of animals. These studies show that unoccupied areas still exist for bears in Scandinavia (**I**) and that the population is likely to continue to grow in numbers as it is estimated to tolerate relatively high rates (10%) of harvest (**V**). One remaining question is whether the population will expand to unoccupied areas and how large populations could be sustained taken the habitat distribution. Our ability to answer this question is at the moment limited by inadequate knowledge about density-dependency in the population dynamics of the bear.

Bayesian estimation of home ranges (**III**) helps in determining effective areas of habitat needed for bear home range establishment. Other studies in the SBBRP have indicated that not only the age and sex of the individual influences the probability of dispersing, but also population density is likely to play a role (Støen et al. 2005a, 2005b). Obviously such social aspects of use of space should be linked with the surrounding habitat structure to really understand the mechanisms of population expansion. Further development of the Bayesian home range estimation by the inclusion of continuous variables, such as distance to other individuals, would enable studying the effect of other individuals in the formation of home ranges. Such improvements in understanding of density-dependent population processes could eventually help in evaluating spatially targeted harvest as a tool for controlling the population.

Traditional radio-tracking data motivated the development of new tools for analysis of habitat use, but it did not allow a detailed study of bear movement paths and dispersal. This is because of the relatively infrequent observations and because dispersing bears were likely to move outside the study area. Thus, an obvious continuation of this work is study of bear dispersal using newly available GPS locations, where the temporal resolution of data is much higher than with radio-tracking. A realistic model of sex-specific dispersal behaviour is one critical missing piece needed for a spatially explicit population model. The individual-based model of study **V** would serve as a platform into which spatial elements could be built into.

Topics addressed in this thesis are all essential components to build a spatially explicit population model for brown bears in Scandinavia. It is of interest for management to be able to project the future distribution of the population while taking into account the development of human activities. The approach of individual-based modelling was chosen particularly because of its potential to incorporate the structure of the landscape and the complicated behaviour of individuals, such as SSI (**IV**), into the model of population dynamics (Grimm 1999, Akçakaya & Sjögren-Gulve 2000, Cramer & Portier 2001, Grimm & Railsback 2005). The harvest model presented here demonstrates the usefulness of simulation models for evaluating effectiveness and likely consequences of different management actions. Combined with the recent developments in techniques for monitoring the bear population size (Bellemain et al. 2005), such models become useful tools for adaptive management. In adaptive management new data will be collected on a regular basis and the model would be re-evaluated and updated based on new information (Mattson et al. 1996).

Although habitat models, together with population models, help us determine the feasibility and consequences of different management goals, the question of what exactly are the goals remains political. Management of human-bear conflicts depends on the political landscape as much as the physical landscape. This work provides grounds for determination of these physical requirements and on further development of a quantitative spatially realistic management-oriented population model of bear dynamics in Scandinavia and Finland.

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